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BROOD VI OF 17-YEAR PERIODICAL CICADAS, *MAGICICADA* SPP. (HEMIPTERA: CICADIDAE): NEW EVIDENCE FROM CONNECTICUT, THE HYPOTHETICAL 4-YEAR DECELERATION, AND THE STATUS OF THE BROOD

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Abstract.—Small emergences of the 17-year periodical cicada, *Magicicada septendecim* (L.), occurred in central Connecticut during 1983. An adult wing and two nymphal exuviae were collected at one site, and the intermittent singing of one to four males was heard at four other localities. The density estimated at one site was only one adult per hectare. Females apparently did not oviposit during 1983. At every locality visited during 1983, there was ovipositional damage caused by females of the sympatric Brood II, which emerged in abundance during 1979. Evidence obtained in 1983 and 1932 (51 years earlier) suggests collectively that Brood VI is not a self-reproducing brood in Connecticut. It is proposed that emergences of Brood VI may be attributed to a few adults of Brood II, which underwent a 4-year deceleration in nymphal development.

A critical examination of early distributional records for Brood VI indicates that the evidence is ambiguous. Misidentifications, developmental flexibility of 17-year periodical cicadas, and records of 13-year cicadas may account for most of the records of Brood VI in the eastern United States. The 4-year deceleration proposed here may be one factor that has contributed to the ambiguity of records of Brood VI and possibly to the formation of cicada broods.

How the many allochronic broods of 13- and 17-year periodical cicadas, *Magicicada* spp., evolved from their ancestral brood(s) is an intriguing question that has stimulated much research. Alexander and Moore (1962), Lloyd and Dybas (1966b), Lloyd and White (1976), and others have hypothesized that the modern broods of periodical cicadas may have originated by 1- or 4-year aberrations in the length of the life cycle. There is evidence that some periodical cicadas have undergone a 4-year acceleration, a 1-year acceleration, or a 1-year deceleration in their developmental time. Dybas (1969) has documented a 4-year acceleration in a portion of the 17-year Brood XIII in the Chicago area. Marlatt (1907, p. 24) has stated that one of his correspondents witnessed a 1-year acceleration of cicadas enclosed in a greenhouse. A 1-year deceleration in development has recently occurred in many *Magicicada* nymphs of Brood XIV in Kentucky (White and Lloyd, 1979). In this paper, I suggest that the cicadas observed in Connecticut during 1932 and 1983 underwent a 4-year deceleration in their nymphal development.

Connecticut is an excellent location for observing unscheduled emergences because only Broods II and XI have been well-documented there (e.g., Marlatt, 1907). Since the nineteenth century, Brood XI has declined rapidly, and it is now apparently

extinct because no adults emerged in 1971 (Manter, 1974). By contrast, the large Brood II has appeared during every scheduled emergence in the twentieth century, most recently in 1979 (Britton, 1912, 1928; Friend, 1946; Leonard, 1964; Maier, 1982a, b). This brood, which in Connecticut has only the species *M. septendecim* (L.), continues to thrive at several localities (Maier, 1980, 1982a, b).

The unexpected emergence of periodical cicadas during 1983 has led to a reexamination of Connecticut collections and literature for overlooked records of Brood VI, which should have emerged in 1983. The search has revealed a record of an emergence 51 years earlier (Anonymous, 1932, p. 232). Unfortunately, this report of Brood VI in the monthly record is omitted from an annual summary and a map of the distribution of Brood VI (Anonymous, 1932, p. 424 and fig.). Britton (1933) corroborated this first report by stating that his staff in Connecticut had collected a few periodical cicadas during 1932. Strangely, he concluded that these adults probably belonged to Brood VII, which was due to emerge in 1933.

The scarcity of adults in 1932 and 1983 suggests that Brood VI does not exist as a self-reproducing brood in Connecticut. Here I propose that these cicadas are actually 21-year-old representatives of Brood II. My hypothesis of a 4-year lengthening of nymphal development will be discussed in relation to hypotheses of brood formation and to the status of Brood VI.

METHODS

In June 1983, five sites in Connecticut were surveyed for the presence of adults and for the egg-laying scars of females. One location in each town of Southington (Hartford Co.), Middlefield (Middlesex Co.), North Branford, Guilford, and Hamden (New Haven Co.) was surveyed for approximately 2 hr per visit. Guilford was inspected on 7 to 9 June and on 15 to 20 June, and the remaining towns were checked once between 9 and 14 June.

Adult density at Southington was estimated on 9 June in the same deciduous forest where Maier (1980, 1982b) recorded the density of Brood II nymphs in 1978 and adults in 1979. To approximate density, the number of singing males was doubled to account for non-singing females; and, this total was divided by the area within the hearing range of the listener. Hearing range was determined by walking away from a singing male until that individual could no longer be heard. The accuracy of the estimate was checked by having two listeners at each location and by using four locations in the forest.

Insect collections housed at The Connecticut Agricultural Experiment Station (New Haven), the Peabody Museum (New Haven) the University of Connecticut (Storrs), and Clemson University (Clemson, South Carolina) were examined for additional specimens collected during the emergence years of Brood VI. All Connecticut specimens collected during 1932 or 1983 are now located in the insect collection of The Connecticut Agricultural Experiment Station.

RESULTS

Adults of *M. septendecim* emerged at each site examined during 1983 (Fig. 1). Two nymphal exuviae (one male, one female) and one adult wing collected in a North Branford yard constituted the physical evidence of the 1983 emergence. The yard

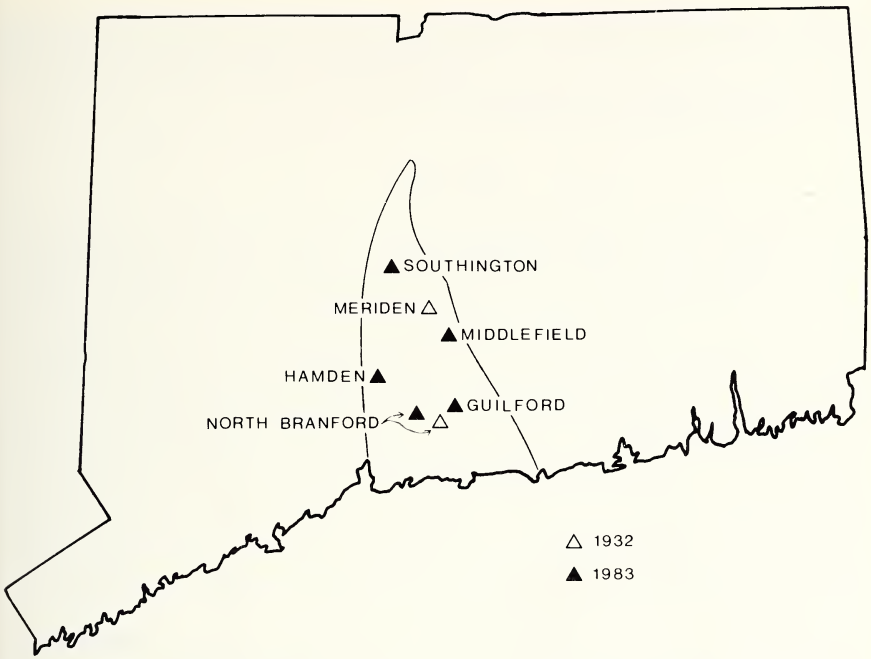

Fig. 1. Distributional records of *Magicicada septendecim* from Connecticut for 1932 and 1983. Each symbol indicates where adults were collected or heard during 1932 (△) or where singing or exuviae were recorded during 1983 (▲). The line encircling the symbols delimits the distributional range of Brood II (modified from Maier, 1982b).

owner, an entomologist, stated that he had struck a live adult and its nymphal exuviae while he was mowing grass on 2 June. A search on 9 June produced the physical evidence to document his observation.

One to four males of *M. septendecim* were singing intermittently at each of the other sites surveyed between 7 and 18 June (Fig. 1). At Guilford, the acoustical records represented three males on 7 June, four males on 8 June, one male on 9 June, three males on 15 June, and one male on 18 June. During each visit between 7 and 15 June, a male was singing in the top of the same sugar maple, *Acer saccharum* Marsh. The number of males heard on 9, 10, or 14 June totaled three at Southington, one at Middlefield, and two at Hamden. The density of adult cicadas at Southington was approximately one per hectare.

Females that emerged during 1983 did not cause any recognizable oviposition damage. However, oviposition scars from 1979 were evident at each of the five sites at which a 1983 emergence of *M. septendecim* was recorded.

Additional records for Marlatt's (1898a) Brood VI were obtained from the insect collection at The Connecticut Agricultural Experiment Station. The collecting dates (20 and 23 June 1932), the location (North Branford), and the collectors (M. Zappe and N. Turner) listed on the labels indicated that these specimens represented most of those upon which Britton (1933) had based his report of a 1932 emergence. In

all, there were ten specimens, including four males, four females (one had a fungal infection of *Massospora*), and two without abdomens. The 1932 collection site in North Branford is located 3 km away and equidistant from the 1983 emergence sites in North Branford and Guilford (Fig. 1).

DISCUSSION

Hypothetical 4-year deceleration. Periodical cicadas that emerged in Connecticut during 1932 and 1983 would be assigned conventionally to Marlatt's (1898a) Brood VI. A typical emergence of Brood VI in the northeastern United States consists of only a few adults (Anonymous, 1932; Hopkins, 1900; Marlatt, 1907). Successful reproduction by sparse populations of adults seems unlikely because small populations of periodical cicadas are usually annihilated by predators (Alexander and Moore, 1962; Chilcote and Stehr, 1984; Karban, 1982; Lloyd and Dybas, 1966a, b). Therefore, I propose that the scarce adults of "Brood VI" from Connecticut actually represent 21-year-old stragglers of the large sympatric Brood II, the only other extant brood in the state. Interestingly, White and Lloyd (1975) did find 19-year-old nymphs in the soil after a major emergence of Brood X in Ohio. If these cicadas survived for two more years, they could have emerged synchronously with the adults of Brood XIV. It is possible, then, that a 4-year deceleration in nymphal development may be responsible for other records of sparse populations.

An alternative hypothesis would be that Connecticut populations of Brood VI are indeed self-reproducing ones, which have dwindled greatly in size due to past 4-year accelerations of members to Brood II. That is, populations of "Brood VI" have reached Lloyd and White's (1976) "phase three." Two problems cast doubt upon this alternative interpretation. First, as mentioned above, successful reproduction by exceedingly small populations is unlikely. This suggestion can be evaluated in 1996 when a sparse population of Brood II is scheduled to emerge at the northernmost Connecticut site recorded by Maier (1982b). At present, however, the rapid demise of Brood XI in Connecticut (e.g., Manter, 1974) serves as a vivid reminder of the fate of a small or local population of *M. septendecim*. Second, given the more than 3 centuries of entomological activity in Connecticut and the possible self-reproduction of this brood, it seems odd that only two emergences of Brood VI have ever been detected in the state.

Hypothetical 4-year decelerations in nymphal development may have contributed to the formation of some of the 17-year broods. For example, let us examine the Broods I and XIV on Long Island. Simon and Lloyd (1982) have hypothesized that Brood XIV is derived from Brood I by 1- and 4-year accelerations (i.e., XIV → X → IX → V → I). Their hypothesis requires four steps whereas the derivation of Brood I from Brood XIV by a 4-year deceleration would require only a single step. Simon and Lloyd (1982) have apparently rejected the possibility of a 4-year deceleration of some members of Brood XIV in favor of a more complex scheme because they had seen no examples of 4-year decelerations and because they had Long Island records for all the broods in their evolutionary scenario. However, their single Long Island record of Brood IX is based on correspondence (Davis, 1920) and therefore must be considered questionable. Moreover, only the abundant Brood XIV and the less abundant Broods I and X are recently well-documented on Long Island. Given the pro-

posed developmental flexibility of 17-year cicadas, I offer the alternate hypothesis that Brood XIV may have produced populations of Broods I and X by 4-year decelerations and accelerations, respectively.

The current theory of brood formation advanced by Lloyd and White (1976) and others draws heavily upon the distributional records summarized by Marlatt (1907). Many of Marlatt's (1907) records are probably ambiguous or erroneous, as I shall demonstrate shortly. Given the apparent developmental repertoire of periodical cicadas, it seems absolutely essential to rely solely upon unambiguous records to support a general theory of brood formation. Consideration of only the unequivocal evidence will surely reduce the number of self-reproducing broods and drastically decrease the distributional range of others.

Status of Brood VI. The question of the validity of Brood VI has concerned Walsh and Riley (1868), Marlatt (1898b), and other students of cicada biology. Distributional data published by the Insect Pest Survey (Anonymous, 1932) and Marlatt (1907) show that Brood VI has the widest range of any 17-year brood. An examination of the evidence, however, indicates that most of the records could be attributed to other broods (e.g., Lloyd et al., 1983; Stannard, 1975) or to other species of cicadas (e.g., Moore, 1966). Fundamental problems with much of the early distributional data are that the limits of 13- and 17-year broods were not fully understood, the variation in the duration of the life cycle was not recognized very often, the species were not identified, and most of the observations were not corroborated with specimens deposited in museums.

Many of the ambiguous records of Brood VI are based on observations conducted in 1881 (Riley, 1881), 1898 (Hopkins, 1900; Marlatt, 1898b, c; Schwarz, 1898), and 1932 (Anonymous, 1932). In the first two years, emergences over large areas could also be attributed to the major 13-year broods that emerged during 1881 (Brood XIX) and 1898 (Brood XXIII). Thirteen-year cicadas of Brood XIX, which underwent a 4-year deceleration in nymphal development, could have emerged during 1898; but, they would have appeared in different areas than would have members of Brood XXIII. Lloyd et al. (1983) and Stannard (1975) have suggested that all Illinois records of Brood VI belong to other broods, such as Brood XXIII. Lloyd et al. (1983) have hypothesized that the 1898 records of Brood VI were actually those of new populations of Brood XXIII, which only became distinguishable as new populations 30 years after members of the "grandparental broods" (X and XIX) hybridized in 1868. Periodical cicadas that emerged in Georgia and the Carolinas during 1932 (Anonymous, 1932) may have been Brood XIX members that accelerated development by 1 year, (Alexander and Moore, 1962), Brood X members that accelerated development by 4 years, or even Brood II members that decelerated development by 4 years.

Outside the distributional range of 13-year broods, records of Brood VI are probably derived mainly from 18-year-old stragglers of Brood V, 21-year-old stragglers of Brood II, or 13-year-old members of Brood X. During each scheduled emergence of Brood VI, 1-year stragglers of Brood V would also have appeared in West Virginia and bordering states. Even though Marlatt (1898c) and Schwarz (1898) recognized that Brood V stragglers probably accounted for many of the Brood VI records, Marlatt (1907) still included these questionable records in his monograph. Continual sympatry of two self-reproducing broods separated by 1 year seems very improbable in

light of recent analyses (Alexander and Moore, 1962; Lloyd and Dybas, 1966b; Lloyd and White, 1976; White and Lloyd, 1979). Clearly, most of the Brood VI records from within the range of Brood V (e.g., Hopkins, 1900) should be assigned to the latter brood. Records of Brood VI from Wisconsin, Indiana, Ohio, Pennsylvania, New York, New Jersey, Maryland, and Virginia could have resulted from 4-year accelerations of Brood X, 4-year decelerations of Brood II, or both. In particular, most of the records of Brood VI from southwestern Wisconsin, northern Indiana, and northwestern Ohio are from counties where Brood X is also recorded (e.g., Anonymous, 1932, 1936; Marlatt, 1907). Similarly, Brood VI emergences in New York, Pennsylvania, and New Jersey tend to be located in counties where Brood II, X, or both have been recorded (e.g., Marlatt, 1907; Simon and Lloyd, 1982).

Convincing evidence of a self-reproducing Brood VI should satisfy the following requirements: (1) An emergence should consist of one or more populations that reproduce successfully. (2) An emergence site should be separated geographically from sites where major broods are scheduled to emerge in the same year or within 1 to 4 years. (3) Adults should emerge at the same location during at least two consecutive emergences. (4) Specimens from each of these consecutive emergences should be deposited in a major insect collection. To date, no published record of Brood VI meets all of these criteria. However, there are intriguing reports of large emergences in 1898 (Marlatt, 1898b) and 1932 (Anonymous, 1932). Sizeable emergences that were reported from Michigan and Wisconsin may have been those of adults of *Okanagana* spp. (Moore, 1966; A. Young, pers. comm., 1983) which resemble adults of *Magicicada* spp. Specimens of *M. septendecim* (one from 1915, six from 1949) collected in three Wisconsin counties are deposited in the collection at the University of Wisconsin at Madison (S. Krauth, pers. comm., 1984). Unfortunately, neither the Wisconsin records nor the Michigan ones completely satisfy criteria 3 and 4.

Large emergences recorded in the Carolinas and Georgia (e.g., Anonymous, 1932; Marlatt, 1907) have occurred in counties located within 200 km of the point where North Carolina, South Carolina, and Georgia meet. These areas seem to be the most promising locations for finding populations of Brood VI, which will meet all of the above requirements. A 1932 emergence in Oconee County, South Carolina is documented with a large series of specimens, which are housed at Clemson University. Because these cicadas emerged within the distributional range of Brood XIX, they were originally identified as *M. tredecim* (Walsh and Riley) adults that had accelerated their development by 1 year (Alexander and Moore, 1962). However, a 1983 emergence documented with two adult females and one nymphal exuviae (examined by me), several reports of large emergences in 1966 (Gorsuch, pers. comm., 1983), and an emergence record from 1881 (Alexander and Moore, 1962) now suggest that the populations in Oconee County may be representatives of a self-reproducing Brood VI. Analyses of wing morphology (Simon, 1983) may provide a means to determine whether these specimens belong to a 13- or 17-year brood. Finally, M. Lloyd (pers. comm., 1984) and C. Simon (pers. comm., 1984) have indicated that they are presently studying self-perpetuating populations of Brood VI in North Carolina. Voucher specimens of *M. septendecim* and *M. septendecula* (Alexander and Moore) from a 1983 emergence in North Carolina are deposited in the collection at North Carolina

State University in Raleigh (C. Parron, pers. comm., 1983). The adults of *M. septendecula* represent the first voucher specimens of this species for Brood VI.

Marlatt's (1907) suggestion that Brood VI is "an assemblage of swarms of diverse origin" has yet to be disproven. Certainly, most of the records from northern states can be attributed to other broods. Records from southern states may prove to be valid ones of Brood VI, but convincing evidence of their authenticity is presently wanting. Ongoing distributional studies (e.g., T. Moore, pers. comm., 1984; C. Simon, pers. comm., 1984) conducted in conjunction with morphometric and enzymic analyses (e.g., Simon, 1979, 1983) may ultimately answer questions about the validity of Brood VI.

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